Journal of Coastal Research	SI	21	197-207	Fort Lauderdale, Florida	Spring 1995

Effects of Hurricane Andrew on Damage and Mortality of Trees in Subtropical Hardwood Hammocks of Long Pine Key, Everglades National Park, Florida, USA

Harold H. Slater,† William J. Platt,‡ David B. Baker,‡ and Hester A. Johnson‡

†aCaribe Research Institute
1034 Gibraltar Road
Key Largo, FL 33037

‡Department of Plant Biology
502 Life Science Building
Louisiana State University
Baton Rouge, LA 70803

ABSTRACT

SLATER, H.H.; PLATT, W.J.; BAKER, D.B., and JOHNSON, H.A., 1995. Effects of Hurricane Andrew on damage and mortality of trees in subtropical hardwood hammocks of Long Pine Key, Everglades National Park, Florida, USA. *Journal of Coastal Research*, SI No. 21, pp. 197-207. Fort Lauderdale (Florida). ISSN 0749-0208.

If hurricane-influenced ecologies exist for terrestrial hardwood forests, then tree damage and mortality due to hurricanes should be systematic since they produce the structure from which aerial sprouts (from either epicormic or axillary buds) arise. This revegetating structure of damaged, yet surviving, trees would strongly influence the inter-competition among survivors (sprouts and advanced recruits) and new recruits (seedlings) in the post-hurricane forest.

The southern inner eyewall of Hurricane Andrew passed directly over the isolated hardwood forests (locally called hammocks) imbedded within the *Pinus ellotii* savannas of Long Pine Key, Everglades National Park on August 24, 1992. Hurricane Andrew caused extensive snapping, uprooting, and defoliation of trees in these hammocks. Four months after Hurricane Andrew, we assessed damage and mortality within six 20 m × 20 m plots randomly placed in the central region of each of three hammocks. In each plot all stems ≥2 cm in diameter believed alive at the time of the hurricane were identified to species, tagged, mapped, and assessed for hurricane damage and mortality.

About 85% of all stems suffered major damage: composed of 45.7% snapped, 22.1% leaning, 9.2% downed, and 7.6% retaining only major branches. Overall, 11.5% of stems ≥2 cm in diameter died. Mortality differed among damage classes: 77.7% of all dead stems were snapped, 10.3% were downed, 7.5% were leaning, 4.1% were standing, and only 0.4% were branched. The mean orientation of downed stems (104°) indicated that most were downed as the southern eyewall passed overhead.

Tree damage and mortality due to Hurricane Andrew was systematically associated with stem size. The proportion of stems (within size classes) that leaned or snapped decreased, while the proportion of stems that became branched or downed increased, as stem size increased. Mortality decreased monotonically with increasing stem size from 13.9% for stems <6 cm in diameter to 3.9% for stems ≥30 cm in diameter. More than 90% of all mortality occurred among stems <10 cm in diameter.

Comparison of windstorm-impacted terrestrial hardwood forests in the Americas indicates that size-related trends in damage are non-random and less variable than size-related trends in mortality. We develop a model that integrates these mortality data. This model predicts that as the uniqueness of a windstorm striking a terrestrial hardwood forest increases, overall mortality increases, and maximum stem mortality occurs at progressively larger stem sizes.

ADDITIONAL INDEX WORDS: *Sprouts, advance recruits, seedlings, stem diameter, windstorm, uniqueness, disturbance.*

INTRODUCTION

The subtropical seasonal hardwood forests, locally called hammocks, of Long Pine Key (LPK), Everglades National Park (Figure 1) are affected less by urban development and contain much smaller exotic plant populations than most other similar forests near the southern tip of the Florida peninsula. This region, at the southern tip of the Florida peninsula, is struck more frequently by hurricanes than any other region of the continental United States (SIMPSON and LAWRENCE, 1971). Landfall frequency is comparable to the high hurricane frequented regions of the Caribbean (NEUMANN *et al.*, 1978). The structure and composition of subtropical seasonal forests in south Florida and the Caribbean may be, in large part, a consequence of frequent hurricanes. In the Americas, subtropical seasonal hardwood forests at 20° N (in the zone of highest hurricane frequency) have similar total basal area as seasonal hardwood forests at

94218 received and accepted in revision 10 November 1994.

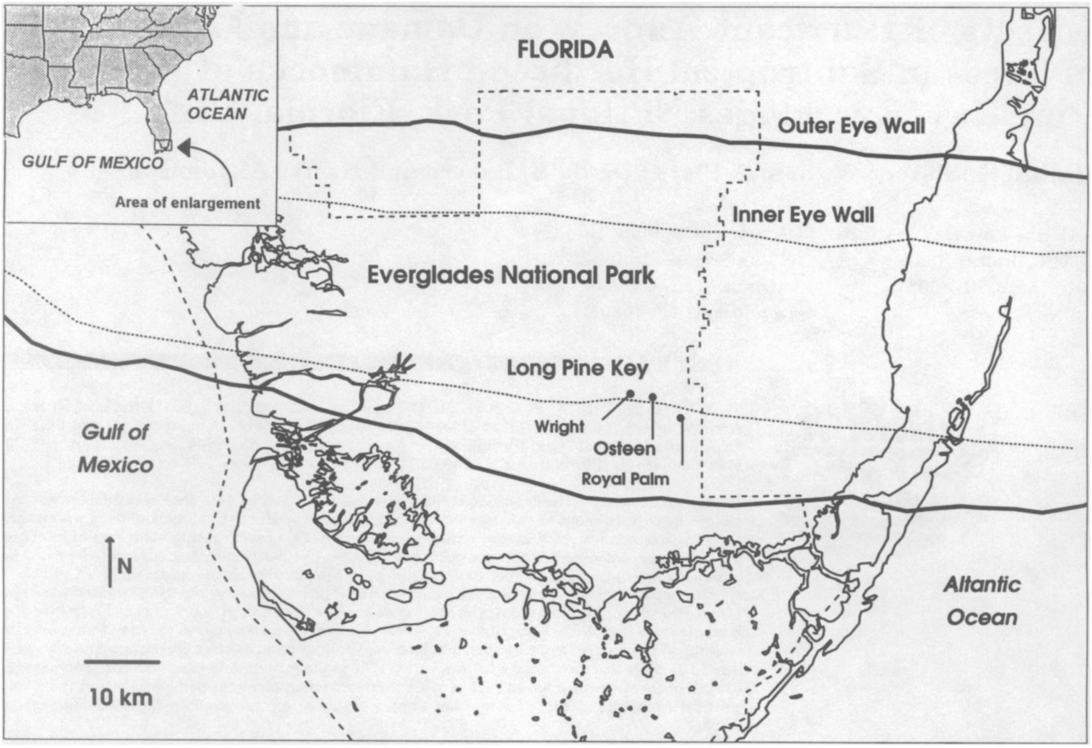

Figure 1. Location of Wright, Osteen, and Royal Palm hammocks (dark circles) within Everglades National Park (dashed lines) at the southern tip of the Florida peninsula relative to the path of the eyewalls (inner eyewalls are dotted lines, outer eyewall are bold lines) of Hurricane Andrew on August 24, 1992.

higher (30° and 40° N) and lower (10° and 0° N) latitudes, but lower proportions of their basal area occur in larger size classes and a greater proportion in smaller size classes (QUIGLEY and PLATT, 1994). In addition, densities of trees and shrubs are much higher at 20° than in seasonal forests at higher or lower latitudes. Such latitudinal differences in size-class structure of forests were hypothesized by QUIGLEY and PLATT (1994) to result from hurricane damage.

Individual trees in the hammocks of south Florida are likely to experience several hurricanes during their life-span (CRAIGHEAD and GILBERT, 1962; GENTRY, 1974), and most tree species found in these hammocks are widely distributed throughout high hurricane frequented regions (TOMLINSON, 1980; Table 1). Thus, these species may each exhibit certain species-specific life history characteristics that allow them to persist in regions frequented by hurricanes, and a later paper will address that topic. However, certain life history characteristics may be common across many species; these may result from systematic damage periodically caused by hurricanes and the uniformity of the post-hurricane forest structure from which vegetation reforms the canopy through sprouting, growth of pre-hurricane juveniles, or germination and growth of post-hurricane seedlings. There may be value in initially ignoring species affiliation and simply noting how the size class structure of forests are affected by hurricanes and whether hurricanes can account for structural differences in these forests relative to those of more northern and southern latitudes (QUIGLEY and PLATT, 1994).

On August 24, 1992, Hurricane Andrew became the latest and strongest known hurricane to alter the vegetation in Everglades National Park, particularly the canopy structure of LPK

Table 1. *Relative abundance of species ≥2 cm in diameter and with at least twenty stems present in the total 0.72 hectare of plots established in Osteen, Royal, and Wright hammocks. Relative basal area is the percent of total stem cross-sectional area (29.25 m^2/ha) contributed by the stems of each species. Relative density is the percent of total stem density (5253 stems/ha) contributed by each species. Frequency is the percent of the eighteen 20 m × 20 m plots in which a species occurs. All listed species are native to south Florida.*

Species	Relative Basal Area (%)	Relative Density (%)	Frequency (%)
Quercus virginiana	28.75	2.1	72
Lysiloma bahamensis	15.67	3.3	78
Metopium toxiferum	10.79	6.3	94
Bumelia salicifolia	9.74	10.9	100
Bursera simaruba	7.24	4.8	100
Coccoloba diversifolia	6.59	16.8	72
Nectandra coriacea	6.20	16.4	100
Exothea paniculata	4.59	8.7	100
Prunus myrtifolia	3.13	5.0	89
Ficus aurea	2.81	1.2	89
Eugenia axillaris	1.58	11.1	100
Simarouba glauca	0.76	0.8	50
Eugenia foetida	0.76	3.4	39
Guettarda elliptica	0.55	4.1	61
Mastichodendron foetidissimum	0.50	0.7	56
Ardisia escallonioides	0.30	3.7	94
Myrsine floridana	0.05	0.6	50

hammocks (OGDEN, 1992). In the current study, we examined whether Hurricane Andrew produced significant size-class based patterns of tree damage and mortality in the hammocks of LPK. We then compared these patterns with those from other hardwood forests of the Caribbean-Gulf of Mexico Basin. We suggest that systematic size-class based patterns of hurricane damage and mortality of trees may strongly influence forest dynamics and result in a characteristic hurricane-related ecology for forests in the Caribbean-Gulf of Mexico Basin.

STUDY SITE

Everglades National Park occupies the southern tip of the Florida peninsula in the USA and experiences alternating wet and dry seasons; its most elevated region (2 m to 4 m above MSL), Long Pine Key (LPK), is the southern most extension of a limestone outcropping called the Miami Rock Ridge (Figure 1). LPK is dominated by a savanna of Dade County slash pine (*Pinus elliottii* var. *densa*); in areas more protected from fire, there are also isolated subtropical hardwood forests called hammocks (CRAIGHEAD, 1974; OLMSTED *et al.*, 1980; OLMSTED *et al.*, 1983; SNYDER *et al.*, 1991). The hammocks of LPK are small (0.5 to rarely 90 ha), with shallow organic debris soils (10 cm to 40 cm) overlying limestone, and their canopies form their densest leaf layers at 4 to 7 m with a discontinuous emergent layer between 10 and 16 m; a substantial subcanopy layer occurs only in areas of disrupted canopy (OLMSTED *et al.*, 1980; OLMSTED *et al.*, 1983; SNYDER *et al.*, 1991). LPK hammocks primarily contain Caribbean hardwood tree species (Table 1) but *Quercus virginiana*, a warm temperate tree species, is also common (OLMSTED *et al.*, 1980; OLMSTED *et al.*, 1983; SNYDER *et al.*, 1991). Hammocks differ greatly in size class distributions of stems and relative abundances of species, possibly because of differences in disturbance histories (OLMSTED *et al.*, 1980).

Three LPK hammocks, located along the path of the southern inner eyewall of Hurricane Andrew, were selected for study. These hammocks (Figure 1), known as Royal Palm, Osteen, and Wright hammocks, are among the larger of the LPK hammocks, each being >20 ha. The hammocks have been previously described (OLMSTED *et al.*, 1983), and differ in size/class structure, species composition, and in the length of time since the last fire (OLMSTED *et al.*, 1980).

Hurricane History of Site

Over the 85 year period from 1886 to 1970, 51 tropical cyclones crossed 250 km of coastline along the southern tip of Florida; these included 33 hurricanes, 12 of which had maximum sustained winds over 200 km/h (SIMPSON and LAWRENCE, 1971; GENTRY, 1974). A number of these hurricanes have influenced the structure of the LPK hammocks. In September 1945, the eye of a hurricane with maximum winds estimated at 275 km/h and a 66 km wide destructive path crossed the northeast corner of the park (SUMMER, 1945). Hurricane Donna moved along the west coast of the park in September 1960, causing defoliation, broken branches and uprooted tress in subtropical forests 50 km to the east (CRAIGHEAD and GILBERT, 1962).

Hurricane Andrew was a category four hurricane when it crossed the southern tip of the Florida peninsula on 24 August 1992 at 16 km/h. Sustained wind speeds were officially estimated at 232 km/h, with gusts to at least 280 km/h (STONE *et al.*, 1993; GRYMES and STONE, 1995). Composite radar imagery (see Armentano *et al.*, this volume) indicated that the southern inner eyewall passed directly over LPK (Figure 1).

METHODS

We censused stem damage within the three selected LPK hammocks during December, 1992, and January, 1993, about four months after the hurricane. Within each hammock, a 70 m × 120 m grid was set up to overlay portions of the plots used in the study of OLMSTED *et al.* (1980). Six 20 m × 20 m plots were placed randomly within the grid. Steel rebar was placed at the corners of each plot. Within each plot we nailed numbered aluminum tags on all stems, excluding lianas, believed alive at the time of the hurricane and ≥2 cm diameter below the lowest major branch (usually about 1 m), or at 1.5 m in height if no lower major branches existed. We measured the diameter of the stem immediately above the tag. We also identified each stem to species, mapped it relative to corners of the plot (see QUIGLEY and SLATER, 1994 for method), and assessed hurricane damage and mortality.

All stems were placed in one of five damage categories, downed, leaning, snapped, branched, or standing. Downed stems were on the ground or leaned <25° relative to the ground; leaning stems inclined between 70° and 25°; snapped stems were broken below all major branches; branched stems retained several of their major branches, each possibly snapped; standing stems remained upright and maintained most secondary branches. We considered stems alive if they had refoliated by 4 months following the hurricane. WALKER (1991) found that most direct hurricane mortality was manifest in Puerto Rican rain forests by this time. We assumed that dead stems in the early stages of bark and wood deterioration were alive at the time of the hurricane. We measured the azimuths of all downed stems ≥10 cm in diameter. An ANOVA, using azimuths converted to radians, was conduced to determine if downed trees in different hammocks varied significantly in their orientation.

We selected eight size classes to assess the association of hurricane damage and mortality with stem size. Four size classes were less than 10 cm in diameter (≥2 cm to <4 cm, ≥4 cm to <6 cm, ≥6 cm to <8 cm, and ≥8 cm to <10 cm) and four were greater than 10 cm in diameter (≥10 cm to <15 cm, ≥15 cm to <20 cm, ≥20 cm to <30 cm, and ≥30 cm). When we averaged stem sizes within a size class, we first calculated the average area of stems in the size class and then converted that average to diameter.

We analyzed the relationships between stem size classes and hammock and damage and mortality and their interactions with cross classification tables using log likelihood ratio chi-square statistics (G-test P values), ANOVAs using F-test P values, MANOVAs using Wilk's λ with its F-test P values, and canonical discriminate analysis. Except for the cross-classification analysis, all analysis used percent data converted by an arcsine square root transformation to normalize model residuals. Each hammock was considered a replicate in the analyses. Size class based mortality was also modeled using standard polynomial regression on transformed percent values. Following analysis of variances and regressions, we verified the univariance and multivariance normality of model residuals. All statistics were performed using SAS for Windows (SAS, 1992).

RESULTS

We tagged and mapped 4072 stems ≥2 cm in diameter (in a total area of 0.72 ha) that were assumed alive at the time of the hurricane. The density of stems in LPK hammocks (5560/ha) resembled stem densities in forests mapped by QUIGLEY and PLATT (1994) at 20° N. Wright hammock contained approximately 36.3% more stems (1650 total or 6880/ha) than either Osteen (1219 or 5080/ha) or Royal Palm (1203 or 5010/ha). In all three hammocks, shapes of size class and distributions of stems were similar (Figure 2). The relative species abundance (Table 1), and distribution of stems among size classes at the time of the hurricane resembled those described by OLMSTED *et al.* (1980). The largest proportions of stems occurred in the smallest size class in all three hammocks; with one substantial exception, progressively smaller proportions of stems occurred in successively larger size classes. A larger proportion of the total number of stems occurred in the ≥10 and <15 cm size class than the ≥8 and

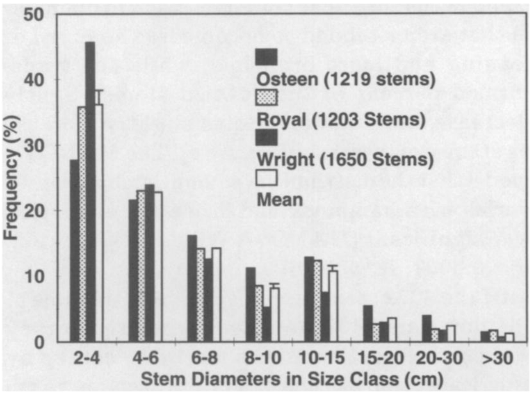

Figure 2. The frequencies (expressed as percent) of all stems in eight size classes in each hammock at the time of Hurricane Andrew. The mean of each size class is presented. 95% confidence intervals are presented as vertical bars where they extend sufficiently beyond the mean to be graphed as distinct line.

<10 cm size class; this reflects the larger size class interval involved. The hammocks differed in the relative distribution of their stems among size classes, primarily as a result of differences in the relative abundance of stems in the smallest size class; this difference was significant (G = 165.5, df = 14, P < 0.001).

Eighty-five percent (approximate) of all stems ≥2 cm in diameter suffered major damage from Hurricane Andrew. Of all trees, 45.7% were snapped, 22.1% were leaning, 9.2% were downed, and 7.6% were branched. Only 15.3% of stems were in the minimum damage category of standing and most of these had lost all leaves and many secondary branches. The relative abundance of damage classes among hammocks differed, primarily to the extent that stems became branched (3.6% of stems in Royal Palm, 6.4% in Osteen, and 11.5% in Wright) or downed (3.6% of stems in Wright, 9.8% in Osteen, and 16.2% in Royal Palm). These differences among hammocks in relative abundance of damage classes were significant in both the cross classification analysis (G = 214.0, df = 8, P < 0.001) and the MANOVA analysis (Wilk's λ $F_{10,20}$ = 3.6, P = 0.008). The average compass orientation of downed stems (104° ± 40°) and its large standard error indicated that while most stems fell as the southern edge of the inner eye wall passed directly overhead, many may have fallen at other times. Hammocks did not differ significantly in this angle of downed stems (ANOVA $F_{2,772}$ = 2.2, P = 0.11).

The type of stem damage incurred during the hurricane was related to stem diameter. The patterns, illustrated in Figure 3, tended to change at sizes between 10 and 20 cm in diameter. Below these sizes, the proportion of stems in a given size class that were snapped or downed tended to increase with increasing size, while the proportions in the leaning or standing categories decreased. The proportion of stems that were branched did not change as size increased. For size classes above the 10–20 cm diameter range, there were slight decreases in the abundance of both downed and leaning stems and large decreases in the abundance of snapped stems. There also were large increases in the proportion of stems that were branched. The overall relationship between stem size and the type of hurricane damage incurred was significant (G = 462.9, df = 28, P < 0.001; MANOVA Wilk's λ $F_{35,45}$ = 3.2, P = 0.0001). Within each damage class, there was significant variation in stem abundance among size classes and hammocks (each damage class had at least G = 28.9, df = 14, P < 0.01), and within each size class, there was significant variation in stem abundance between damage class and hammock (each size class had at least G = 16.8, df = 8, P < 0.03).

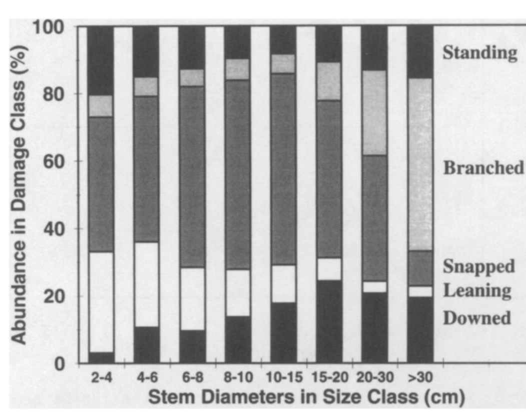

Figure 3. The proportions of trees in a given size class (expressed as percent of trees in that size class) that experienced damage of a given category. All trees were placed into one of five damage categories (standing, branched, snapped, leaning, downed). Data were obtained by averaging across all three hammocks.

The canonical discriminate analysis plot (Figure 4) illustrates that the size-related damage class patterns depicted in Figure 3 are consistent within hammocks and non-random. The means of progressively larger size classes of the arcsine square root damage class data, averaged across hammocks, trace a consistent trajectory through the Cartesian plane form by the first two canonical axes. These two canonical dimensions accounted for 97.8% of the variation in the damage data (58.1% and 39.7% for the first and second axis, respectively), and both axes are significant (the null hypothesis that the canonical correlation of the second canonical axis and all additional ones equal zero has a P value of 0.03). The trajectory formed by progressively larger size classes is interpretable by projecting damage class vectors, formed by multiplying the correlation coefficient of each damage class with each canonical axis and the eigenvalue of that axis, on to the canonical Cartesian plane. The interpretation of the size by damage class trajectory in Figure 4 is similar to that given above for Figure 3. As stem size increased through the first five of the eight size classes, bracketing 2 cm to 15 cm diameter, the transformed percent of the stems snapped or downed tended to increase and that of stems leaning or standing tended to decrease; the branched category remained unchanged. The trend in the three size classes ≥15 cm in diameter is that stems tended to become less snapped or leaning and more branched, while the transformed percent of the downed stems slightly decrease and standing stems slightly increase as stem size increases (Figure 4). The MANOVA model that the distribution among damage classes varies with hammock and size class affiliation was significant (MANOVA Wilk's λ $F_{35,53} = 3.2$, $P = 0.0001$, $R^2 = 0.56$).

Of the 4072 stems assumed alive at the time of the hurricane, 467 were dead when the survey was conducted. Short-term mortality caused by Hurricane Andrew thus was 11.5% of stems ≥2 cm in diameter over all three hammocks. There was a significant linear relationship between the mean diameter of stems in the different size classes (each hammock considered separately) and the transformed mortality of stems in those size classes (ANOVA $F_{1,22} = 22.2$, $P = 0.0001$, $R^2 = 0.5$). We back-transformed this relationship for presentation in Figure 5. The mortality of size classes decreased from a high of 13.9% in the first two size classes (bracketing from ≥2 cm to <6 cm in diameter) to a low of 3.9% for the largest size class (≥30 cm).

The proportion of all mortality that occurred in the different size classes (all hammocks com-

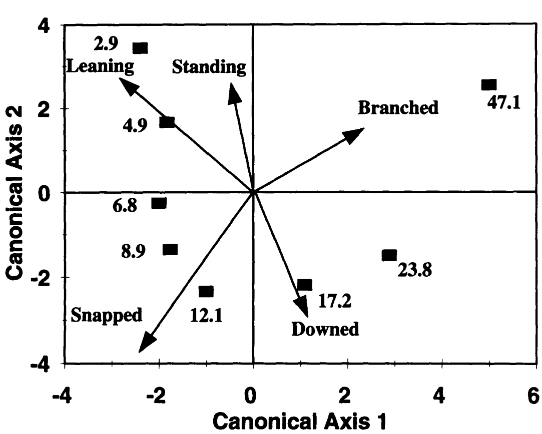

Figure 4. Canonical discriminate analysis of the transformed percent occurrence of trees in different damage categories for each size class, averaged across hammocks. The average diameter (cm) of each size class is placed next to the black squares identifying the position of that size class in the damage space. Arrows represent vectors for each damage class, created by multiplying the eigenvalue of each transformed damage class by its correlation coefficient with each canonical axis.

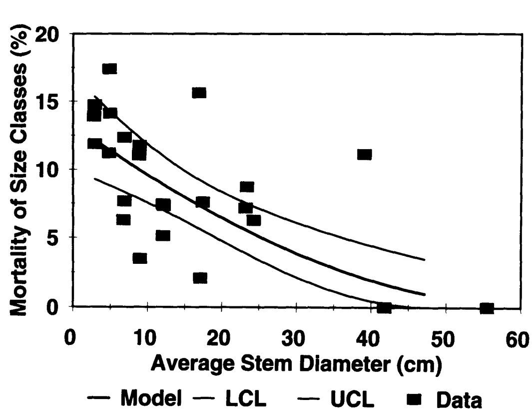

Figure 5. The proportion of trees within each size class (expressed as percent) in each hammock that were dead four months after Hurricane Andrew is graphed (black squares) in relation to the mean diameter of trees in each size class in each hammock. The lines represent the back transformed best-fit linear mortality model; these lines represent the mean (bold) and the upper and lower 95% confidence intervals of the best-fit linear model.

bined) is illustrated in Figure 6. The proportion of mortality mirrored the size class distribution in that mortality decreased rapidly in successively larger size classes (except in the ≥ 10 and <15 cm size class). The four smallest size classes, those <10 cm in diameter, contain 90% of all dead stems. The linear decrease in mortality was significant ($G = 40.1$, $df = 7$, $P < 0.001$, Figure 6).

The mortality associated with the different damage classes also is illustrated in Figure 6. Mortality was not uniform among damage classes, 77.7% of all dead stems were snapped, 10.3% were downed, 7.5% were leaning, 4.1% were standing, and only 0.4% were branched. These differences were significant (G = 286.6, df = 4, P < 0.001; ANOVA $F_{4,106}$ = 27.1, P = 0.0001). There were, however, no significant differences in relative mortality among hammocks ($G = 5.5$, $df = 2$, $P = 0.063$; ANOVA $F_{2,106} = 0.53$, $P = 0.59$). There were differences in the distribution of mortality among damage classes for the different size classes (Figure 6; $G = 61.2$, $df = 28$, P < 0.001). These differences reflected the changes with size in the proportion of trees that occurred in the most severe damage categories (*i.e.*, snapped and downed).

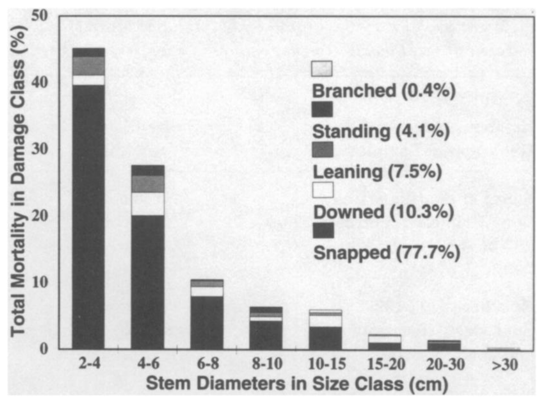

Figure 6. The distribution of total mortality four months after Hurricane Andrew among the eight size classes (expressed as percentage of total mortality) and the five damage categories. Averages are across all three hammocks, and the percent of total mortality in each damage category is presented in parentheses.

DISCUSSION

If hurricane-influenced ecologies exist for terrestrial hardwood forests, then hurricanes should be both frequent (multiple occurrences within the lifespans of trees) and somewhat systematic in the damage and mortality they inflict on trees. Systematic patterns of tree damage and mortality would produce a characteristic post-hurricane forest structure from which aerial sprouts (from either epicormic or axillary buds) could predictably arise along the damage stems that make up this structure. This structure would refoliate in a high light environment, and would strongly influence microclimate and interactions among survivors (sprouts and advance recruits) and new recruits (seedlings). Consequently, production of aerial sprouts from severely damaged stems should be selected in forests such as the hammocks of LPK that periodically experience hurricanes.

The structure of each LPK hammock examined was altered in similar ways by Hurricane Andrew. Essentially all foliage and secondary branches and many of the primary branches of the canopy were removed. However, few stems were killed outright by the storm (11.5%) and only 10% of these had uprooted. Instead, most trees that formed the canopy prior to the hurricane survived by producing epicormic branches along their severely damaged stems. Four months after the hurricane, some species had aerial sprouts one meter in length.

Systematic size-related patterns of hurricane damage and mortality emerge when we compare forests of the Caribbean-Gulf of Mexico Basin that have recently experienced hurricanes (Table 2). These forests, the subtropical hammocks of LPK, the warm-temperate forests of the upper Gulf of Mexico (PLATT *et al.*, 1995), and the tropical forests of southeastern Nicaragua (BOUCHER *et al.*, 1990; YIH *et al.*, 1991) have almost no species overlap and their canopies are of different heights; however, these forests are similar in that they are composed of relatively fast-growing hardwood trees. Hurricanes affect stem diameter in these hardwood forests. Stems snap more often than they are downed, larger stems snap less frequently than smaller stems, and downed stems increase in abundance until they reach intermediate stem size. Their abundance either remains unchanged or decreases as stem size increases (Table 2). WALKER (1991), working in similar hardwood forests of Puerto Rico, also found that damage among stems ≥ 5 cm was partly explained by stem diameter: uprooted

Table 2. *Hurricane damage and mortality of trees in hardwood forests at three regions of the Caribbean-Gulf of Mexico Basin. The size classes for our data were altered to make them compatible with the other studies presented in this table. Data from different authors are separated by blank lines. Mortality within a size class is indicated by enclosing it in parentheses ( ). Percent of total mortality that occurs in each size class is indicated by enclosing it in brackets [ ].*

Reference Location Wind Speed; Sample Size	Size Classes (cm dbh)	Total Stems in Size Class	Size Class Mortality (%)	Standing % of Size Class	Snapped % of Size Class	Downed % of Size Class
Slater *et al.*, this article	≥5 to <16	1762	[91.5] (9.2)	(4.1) 34.5	(12.2) 52.4	(10.4) 13.1
Long Pine Key, Southern Florida	≥16 to <31	206	[7.3] (6.3)	(2.5) 38.3	(7.1) 40.8	(11.6) 20.9
232 km/h; $N = 2019$	≥31 to <46	27	[1.1] (7.4)	(0.0) 55.6	(33.3) 11.1	(11.1) 33.3
	>46	19	[0.0] (0.0)	(0.0) 73.7	(0.0) 15.8	(0.0) 10.5
Boucher *et al.*, 1990	≥5 to <16	75	[38.9] (9.3)	(0.0) 30.7	(16.1) 41.3	(9.5) 28.0
Southeast Nicaragua	≥16 to <31	44	[33.3] (13.6)	(0.0) 13.6	(8.3) 54.5	(28.6) 31.8
260 km/h; $N = 140$	≥31 to <46	14	[22.2] (28.6)	(0.0) 14.3	(20.0) 35.7	(42.9) 50.0
	>46	7	[5.6] (14.3)	(0.0) 57.1	(0.0) 14.3	(50.0) 28.6
Yih *et al.*, 1991	≥5 to <16	NR[a]	[NR] (20.0)	(NR) NR	(NR) NR	(NR) NR
Southeast Nicaragua	≥16 to <31	NR	[NR] (41.0)	(NR) NR	(NR) NR	(NR) NR
260 km/h; $N = 374$	≥31 to <46	NR	[NR] (58.0)	(NR) NR	(NR) NR	(NR) NR
	>46	NR	[NR] (0.0)	(NR) NR	(NR) NR	(NR) NR
Platt *et al.*, 1995	≥2 to <16	1480	[66.7] (4.7)	(1.9) 67.4	(9.1) 22.9	(14.0) 9.7
North Florida and Southern Georgia	≥16 to <31	359	[15.2] (4.5)	(0.5) 57.1	(9.0) 21.7	(10.5) 21.2
160 km/h; $N = 2255$	≥31 to <46	154	[5.7] (3.9)	(0.0) 64.9	(9.5) 13.6	(12.1) 21.4
	>46	262	[12.4] (5.0)	(0.0) 61.5	(14.7) 13.0	(11.9) 25.6

[a]NR = Value is not reported in article, or determinable.

stems were significantly larger than intact or snapped stems. As in our study, this trend did not exist when the only stems examined were ≥10 cm in diameter (WALKER *et al.*, 1992).

Size-related patterns of windstorm-induced tree mortality are more variable than patterns of tree damage. We propose a graphical model (Figure 7) to integrate admittedly limited data on windstorm-induced stem mortality in terrestrial hardwood forests as a function of stem size. The goal of the model was to predict approximate levels and size-class based patterns of mortality, not the exact mortality incurred by given stem sizes in any windstorm. Our model states that as the uniqueness of a windstorm striking a terrestrial hardwood forest increases, overall mortality increases, and maximum stem mortality occurs at progressively larger size classes. We define windstorm uniqueness by example. If forests experience windstorms of similar intensity, uniqueness is greater in forests where the frequency of windstorms is lower; when forests experience similar windstorm frequencies, uniqueness increases as windstorm intensity increases. Thus uniqueness is ordinal in our model and is a one-dimensional representation of a two-dimensional phenomenon involving windstorm frequency and intensity.

The study by PLATT *et al.* (1995) documented the least unique windstorm summarized in Table 2. It was a moderate intensity windstorm striking a high windstorm frequented region (SIMPSON and LAWRENCE, 1971) and mortality shows little trend as stem size increases (profile A in Figure 7). Our study of LPK hammocks is of a high intensity windstorm striking a high windstorm frequented region (SIMPSON and LAWRENCE, 1971). Its higher intensity made its uniqueness exceed that of PLATT *et al.* (1995); thus mortality was higher, and it exhibited a definite trend; mortality decreased monotonically as stem size increased (profile B in Figure 7). BOUCHER *et al.* (1990) and YIH *et al.* (1991) described a windstorm equal in intensity to Hurricane Andrew at LPK which struck a region of lower hurricane frequency than either LPK or most Caribbean forests (NEUMANN *et al.*, 1978); thus, its uniqueness exceeded that of Hurricane Andrew at LPK, its overall mortality was greater, and its greatest mortality was at an intermediate size class (profile C in Figure 7). Hardwood forests in the upper Midwest of the

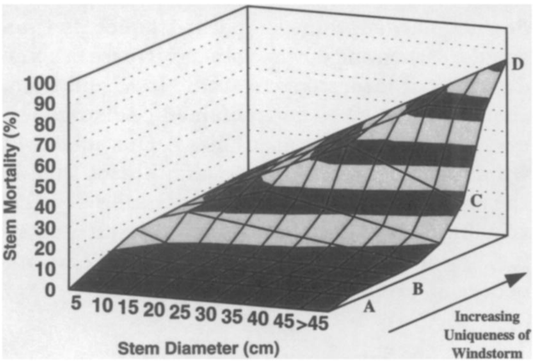

Figure 7. Theoretical model of stem mortality (expressed as percent of trees in a given size class) as a function of size in terrestrial hardwood forests differing in the uniqueness of windstorms. The uniqueness of any given windstorm for any given forest depends on frequency and intensity of windstorms occurring over time (see text for details). The model topography is split into 10% mortality contours. Size class based mortality profiles are from the following studies (listed in Table 2) and indicated on the graph by capital letters: (A) Platt *et al.* (1995); (B) Slater *et al.* this paper; (C) Boucher *et al.* (1990) and Yih *et al.* (1991); (D) Dunn *et al.* (1983).

USA experience a very low frequency of intense windstorms (DUNN *et al.*, 1983), and our model predicts that the stem size based mortality profile will approach that of profile D in Figure 7. Although DUNN *et al.* (1983), who documented an intense thunderstorm downburst (253 km/h maximum winds) in a Wisconsin Hemlock-Hardwood forest, did not report detailed stem size based mortality, their data shows that sapling (≥2.5 cm to <10 cm in diameter) density did not appreciably change, and thus their mortality was much lower than that of trees (≥10 cm in diameter) which suffered 89% mortality. Contrast these results to those of GLITZENSTEIN and HARCOMBE (1988) who also documented a non-hurricane windstorm. This east Texas floodplain forest, the Turkey Creek Unit, was struck by a tornado (250 km/h maximum winds), and it exists in a region more frequented by windstorms than the forest documented by DUNN *et al.* (1983). Thus, this windstorm was less unique and the forest suffered less mortality (14.4% for stems ≥2 cm and 55.5% ≥10 cm in diameter). Its mortality profile would lie between profiles C and D in Figure 7.

Certain tree species have well-documented resistance to windstorm damage; for example, cypress (TOULIATOS and ROTH, 1971; GRESHAM *et al.*, 1991; NOEL *et al.*, this volume). In hurricane-frequented subtropical forests comprised of rapidly growing species of trees, differences in recovery through aerial sprouting from damaged stems are more likely to control post hurricane canopy structure and composition than differences in resistance to wind damage (BROKAW and WALKER, 1991; YIH *et al.*, 1991; WALKER *et al.*, 1992; and this study). Hence major post-hurricane changes in species composition of canopies appear unlikely in these forests (see YIH *et al.*, 1991). The existence of sprouting from damage structure is the common mechanism by which species maintain their presence in the canopies of these forests following a hurricane. This indicates that there has been past selection for rapid sprouting (from abundant dormant buds) and rapid regrowth of damaged stems of those tree species that occur in hurricane-frequented subtropical forests of the Caribbean region. This trend exists in spite of the different species composition of these forest canopies.

Those patterns described by QUIGLEY and PLATT (1995) for seasonal forests at 20° N, including higher densities of stems and lower abundances of canopy trees, are consistent with the patterns of mortality, as well as those of damage and refoliation occurring in LPK hammocks at 25° N, and many other hardwood forests of the Caribbean–Gulf of Mexico Basin. Low direct mortality from hurricanes would result in trees living through several such storms and being defoliated and damaged to varying degrees by repeated hurricanes. Repeated damage would depress the basal area and density of canopy trees relative to those of sub-canopy trees and shrubs (see QUIGLEY and PLATT, 1995). Sprout production and rapid growth in the high light of the post-hurricane forest would result in high densities of trees and multiple stems as well-defined characteristics of these hurricane-frequented subtropical forests (see QUIGLEY and PLATT, 1995).

Hurricane Andrew inflicted a level of damage to the hardwood hammocks of LPK approaching the upper end of the damage that hurricanes potentially inflict. As such, the reported damage exceeds that recorded by most studies of hurricane damage to terrestrial hardwood forests (but similar to BOUCHER *et al.*, 1990 and YIH *et al.*, 1991). The severe alteration of the canopy structure of LPK hammocks due to Hurricane Andrew places them at a spatial scale of damage beyond similarity to a treefall gap (as suggested by the graphical model developed by a recent workshop on the ecological effects of hurricanes; ACKERMAN and WALKER, 1991). Given that these subtropical hardwood forests were located beneath the hurricane eyewall and thus experienced extreme wind forces and damage and that site factors were mostly irrelevant, the gap model of ACKERMAN and WALKER (1991) would predict that recovery of LPK hammocks will require centuries. Since trees in hammocks of LPK experienced low mortality and are currently sprouting and regrowing at rapid rates, they can be expected to reform intact hammock canopy structure resembling that prior to the hurricane within a few decades, not centuries. The data from these forests support the hypothesis of DENSLOW (1985) that ecological systems experiencing frequent disturbances require less time to recover. Nonetheless, recovery is a relative state, because the likelihood of redisturbance by yet another hurricane is likely within that same period of time as recovery from the most recent hurricane.

CONCLUSION

Hurricane Andrew radically altered the canopy structure of the subtropical hardwood hammocks of Long Pine Key. The overall level of tree damage was severe (85% suffered major damage) but mortality was low (11.5%), and the type of damage and level of mortality changed as trees increased in stem diameters. As stem diameter increased from 2 cm to 15 cm, the percent of the stems that snapped or became downed tended to increase and fewer leaned. Trees >15 cm in diameter tended to snap or lean less and were more likely to be branched as stem diameter increased and were slightly less likely to be downed. Mortality decreased monotonically as stem diameter increased, from 14% for small trees to a low of 4% for the largest trees.

Comparison of the type and magnitude of damage and levels of mortality caused by Hurricane Andrew in LPK hammocks to that produced by windstorms in similarly structured hardwood forests of the Caribbean-Gulf of Mexico Basin indicates that certain size-based trends exist. Stem size based patterns of damage from windstorms are more uniform in forests differing in the uniqueness of windstorms than are mortality patterns. Trees snap more often than they are downed, larger stems snap less frequently than smaller stems, and downed stems increase in abundance until intermediate stem sizes, and then, their abundance either remained unchanged or decreased at larger stem sizes. Our model of windstorm caused tree mortality states that as the uniqueness of a windstorm striking a terrestrial hardwood forest increases, overall mortality increases, and maximum stem mortality occurs at progressively larger stem sizes.

ACKNOWLEDGMENTS

Research conducted as part of the current study was funded by National Science Foundation grants BSR-9123196 (W.J. PLATT & H.H. SLATER, PIs) and DEB-9314265 (W.J. PLATT, PI), National Park Service Cooperative Agreement 5280-4-9005 (H.H. SLATER & W.J. PLATT, PIs), and the South Florida Research Center.

LITERATURE CITED

ACKERMAN, J.D. and WALKER, L.R., 1991. Ecological effects of hurricanes. *Bulletin of the Ecological Society of America*, 72, 178–179.

ARMENTANO, T.; DOREN, R.F.; PLATT, W.J., and MULLINS, T., 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. *Journal of Coastal Research*, SI No. 21 (this issue).

BOUCHER, D.H.; VANDERMEER, J.H.; YIH, K., and ZAMORA, N., 1990. Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology*, 71, 2022–2024.

BROKAW, N.V. and WALKER, L.R., 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica*, 23, 442–447.

CRAIGHEAD, F.C., 1974. Hammocks of south Florida. *In*: GLEASON, P.J. (ed.), *Environments of South Florida: Present and Past II*. Miami: Miami Geological Society, Memoir II, pp. 53–60.

CRAIGHEAD, F.C. and GILBERT, V.C., 1962. The effects of Hurricane Donna on the vegetation of southern Florida. *The Quarterly Journal of the Florida Academy of Sciences*, 25, 1–28.

DENSLOW, J.S., 1985. Disturbance-mediated coexistence of species. *In*: PICKETT, S.T.A. and WHITE, P.S. (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Orlando, Florida: Academic Press, Inc.

DUNN, C.P.; GUNTENSPERGEN, G.R., and DOMEY, J.R., 1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. *Canadian Journal of Botany*, 61, 211–217.

GENTRY, R.C., 1974. Hurricanes in south Florida. *In*: GLEASON, P.J. (ed.), *Environments of South Florida: Present and Past II*. Miami: Miami Geological Society, Memoir II, pp. 510-518.

GLITZENSTEIN, J.S. and HARCOMBE, P.A., 1988. Effects of the December 1983 tornado on forest vegetation of the Big Thicket southeast Texas, U.S.A. *Forest Ecology and Management*, 25, 269-290.

GRESHAM, C.A.; WILLIAMS, T.M., and LIPSCOMB, D.J., 1991. Hurricane Hugo wind damage to southeastern U.S. coastal forest tree species. *Biotropica*, 23(4a), 420-426.

GRYMES, J.M. and STONE, G.W., 1995. A review of key meteorological and hydrological aspects of Hurricane Andrew. *Journal of Coastal Research*, SI No. 21 (this volume).

NEUMANN, C.J.; CRY, E.L.; CASO, E.L., and JARVINEN, B.R., 1978. *Tropical Cyclones of the North Atlantic Ocean, 1871-1977*. National Climatic Center, National Oceanic and Atmospheric Administration. Asheville, North Carolina.

NOEL, J.M.; MAXWELL, A.; PLATT, W.J., and PACE, L., 1995. Effects of Hurricane Andrew on cypress (*Taxodium distichum* var. *nutans*) in south Florida. *Journal of Coastal Research*, Special Issue No. 18 (this volume).

OGDEN, J.C., 1992. The impact of Hurricane Andrew on the ecosystems of south Florida. *Conservation Biology*, 6, 488-490.

OLMSTED, I.C.; LOOPE, L.L., and HILSENBECK, C.E., 1980. Tropical hardwood hammocks of the interior of Everglades National Park and Big Cypress National Preserve. *South Florida Research Center Report T-604*, 58p.

OLMSTED, I.C.; ROBERTSON, W.B., Jr., and BASS, O.L., Jr., 1983. The vegetation of Long Pine Key, Everglades National Park. *South Florida Research Center Report SFRC-83/05*, 64p.

PLATT, W.J.; BREWER, J.S.; GRACE, S.L.; OLSON, M.S.; SLATER, H.H., and QUIGLEY, M.F., 1995. The Impact of Hurricane Kate on Old-growth Southeastern Coastal Plain Forests (unpublished manuscript).

QUIGLEY, M.F. and PLATT, W.J., 1995. Latitudinal changes in the structure of seasonal forests. *Ecology*, 18, 133-136.

QUIGLEY, M.F. and SLATER, H.H., 1994. Mapping forest plots: a fast triangulation method for one person working alone. *Southern Journal of Applied Forestry*, 18, 133-136.

SAS, 1992. *SAS/STAT User's guide*. Cary, North Carolina: SAS Institute Inc., Volumes 1 & 2.

SIMPSON, R.H. and LAWRENCE, M.B., 1971. *Atlantic hurricane frequencies along the U.S. coastline*. National Oceanic and Atmospheric Administration Technical Memorandum NWS SR-58, 14p.

SNYDER, J.R.; HERNDON, A., and ROBERTSON, W.B., Jr., 1991. South Florida rockland. *In*: MYERS, R.L. and EWEL, J.J. (eds.), *Ecosystems of Florida*. Orlando: University of Central Florida Press.

STONE, G.W.; GRYMES, J.M.; ROBBIN, K.; UNDERWOOD, S.G.; STEYER, G.D., and MULLER, R.A., 1993. A chronological overview of climatological and hydrological aspects associated with Hurricane Andrew and its morphological effects along the Louisiana coast, U.S.A. *Shore and Beach*, 61(2), 2-12.

SUMMER, H.C., 1945. North Atlantic hurricanes and tropical disturbances of 1945. *Monthly Weather Review*, 74, 1-5.

TOMLINSON, P.B., 1980. *The biology of trees native to tropical Florida*. Allston, Massachusetts: Harvard University Printing Office, 480p.

TOULIATOS, P. AND ROTH, E., 1971. Hurricanes and trees: ten lessons from Camille. *Journal of Forestry*, 69, 285-289.

WALKER, L.R., 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 23, 379-385.

WALKER, L.R.; VOLTZOW, J.; ACKERMAN, J.D.; FERNANDEZ, D.S., and FETCHER, N., 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology*, 73, 691-694.

YIH, K.; BOUCHER, D.H.; VANDERMEER, J.H., and ZAORA, N., 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica*, 23(2), 106-113.